Biomere boundaries in the Phanerozoic time scale

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Abstract. Abrupt nonevolutionary changes in the fossil record of trilobites during the Cambrian, without associated evidence of lithologic changes or discontinuities, are known as biomere boundaries. We suggest that biomere boundaries are more widespread in the Phanerozoic time scale than previously reported. Accordingly we have expanded the original biomere concept to include nonevolutionary biotic changes, involving one or more phyla, that are the results of major environmental changes of local or worldwide extent. The effects of these changes on benthic taxa are nearly synchronous on the craton and diachronous in shelf and slope environments. The Ordovician-Silurian boundary may provide an example of this type of biomere boundary as indicated by changes in biota. The existence of a biomere boundary rather than a synchronous time boundary at the traditional Ordovician-Silurian systemic boundary, would indicate that there is a significant amount of time equivalency between the Ashgillian and Llandoverian.

INTRODUCTION

A major focus of the earth sciences since the time of William Smith has been the development and continued refinement of the geologic time scale. Numerous difficulties have been encountered, but evidence of considerable progress and standardization recently has been published (Hedberg, 1976; Cohee et al., 1978). Major chronostratigraphic units (system, series, etc.) and corresponding geochronologic units (period, epoch, etc.) of this time scale have been established on a global scope; by definition, these units have isochronous boundaries. The boundaries of chronostratigraphic units are best defined by well-documented changes in the fossil record. Ideally, these changes are recognized by lineage biozones, based on first occurrences of fossil taxa established at a stratotype section for each boundary (Committee on the Silurian-Devonian Boundary and Stratigraphy, 1972; Murphy, 1977). In practice, most boundaries and especially system boundaries are poorly defined and difficult to correlate on a global scale. We propose herein that a major obstacle to regional and global correlation of some system boundaries (e.g., Cambrian-Ordovician, Ordovician-Silurian, Permian-Triassic, Cretaceous-Paleogene, etc.) is that they are not isochronous as traditionally assumed, but rather represent intervals of time manifested by biomere boundaries and therefore are diachronous. Consequently they do not meet the requirements of synchronous time-stratigraphic boundaries. Biozones previously recognized as representing the upper part of one system (e.g., Ordovician) and those representing the lower part of the overlying system (e.g., Silurian) may be partly or completely time equivalent where they are transected by a biomere boundary. We believe the interval of time for the total duration of a biomere boundary is considerably greater than the interval of time necessary for simple faunal migrations—an interval traditionally considered insignificant by stratigraphers (*see* sections on Biomere Boundaries and Ordovician-Silurian Boundary).

The purpose of this paper is to expand the concepts of biomere and biomere boundaries as originally defined by Palmer (1965a) and to apply the expanded concepts to systemic boundaries. We do not intend to prove that the Ordovician-Silurian boundary is a biomere boundary; rather we point out an alternative explanation for the

existing data and indicate how this interpretation would affect attempts at regional correlation. The concepts presented here are not restricted to the Ordovician-Silurian boundary but also may apply to other time-stratigraphic boundaries in the Phanerozoic.

BIOMERE BOUNDARIES

Biomeres were first defined on the basis of the stratigraphic distribution of Late Cambrian trilobites in the Great Basin (Palmer, 1965*a*, 1965*b*). They represent ". . . a regional biostratigraphic unit bounded by abrupt nonevolutionary changes in the dominant elements of a single phylum. These changes are not necessarily related to physical discontinuities in the sedimentary record and they are, or may be, diachronous." Subsequent work on the recognition of biomeres and biomere boundaries has been sparse, but they have been recognized in collections of Late Cambrian trilobites from Texas and Oklahoma (Longacre, 1970; Stitt, 1971*a*, 1971*b*). Changes in Late Cambrian conodonts and inarticulate brachiopods closely correspond with the changes in trilobites reported from the Great Basin (Rowell and Brady, 1976). More recent evidence in support of the biomere concept was provided by the changes in trilobites from a very detailed measured section in the Great Basin (Palmer, 1979).

The changes in trilobites between biomere boundaries were classified into four stages (not chronostratigraphic) by Stitt (1971*a*, 1971*b*); Palmer (1979) has recently modified Stitt's faunal stages. As most recently described by Palmer (1979), stage one of a biomere follows immediately after a major crisis eliminates most of the existing benthic trilobite taxa, and it is characterized by very low diversity and high abundance of generalist species. Stage two represents an initial evolutionary radiation of remaining stocks and contains relatively short ranging taxa. Stage three is represented by a decrease in diversity and establishment of new major taxonomic groups. In stage four, trilobites again increase in diversity to fill most or all habitats; this climax in diversity is followed by another crisis. Taylor (1977) and Palmer (*personal communication*) suggested that Cambrian biomeres were produced by the rising of the thermocline and consequent rapid extinction of warm-water, shelf trilobites; new stocks of colder, deeper-water trilobites subsequently migrated into the depauperate habitats on shelf areas and then underwent adaptive radiations. Of interest is the fact that no biomeres have yet been formally proposed in rocks younger than Cambrian (500 m.y.) in age.

A significant new stratigraphic concept is available if the original concept of biomere is expanded as follows: 1) biotic changes at biomere boundaries are due to major environmental changes of local or worldwide extent; 2) biotic changes may affect one or more phyla; 3) in cratonic seas these changes may appear to be essentially synchronous (Palmer, 1978), whereas in offshore (shelf or slope) environments the changes may be diachronous; and 4) the diachroneity of a biomere boundary may span millions of years (discussed below). This expanded concept of a biomere may provide a more accurate explanation for many erathemic or systemic boundaries previously considered synchronous, unconformable, or paraconformable.

We believe that the diachroneity of a biomere boundary may span millions of years (point 4 of above). Our belief is based on faunal patterns of the Ordovician-Silurian boundary (*see* following section on the Ordovician-Silurian boundary) and the nature of the invading stock. The invading stock originates from genetically conservative, deeper-water faunas. The genetically conservative nature of the group is suggested by 1) the morphological similarity between invading stocks of different biomeres (Palmer, 1965*a*), suggesting a common basic stock for the invading trilobites which were evolving much slower than the contemporaneous shallow-water taxa; 2) the less dense populations in modern deep-sea environments (Ingle, 1975; Wigle and Emery, 1967) because it is harder to find a mate; 3) the reduction in egg numbers, K-mode reproduction, in modern deep-sea faunas (Allen, 1979; Sanders, 1979; Rex, 1979); and 4) the extreme lengths of time between generations due to the "late" sexual maturity of modern deep-water faunas (Allen, 1979; Sanders, 1979; Rex, 1979).

For a genetically conservative invading stock to migrate from the stable, colder,
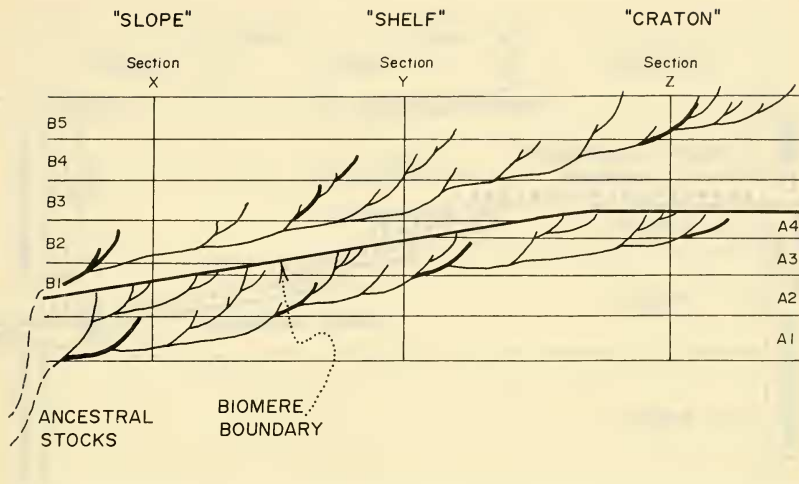
"SLOPE"   "SHELF"   "CRATON"

FIGURE 1. Generalized concept of a biomere boundary. A1 through A4 and B1 through B3 represent lineage biozones based on benthic or nekto-benthic organisms. Evolution of "group" A continues in onshore areas not yet affected by environmental change. Lineage B taxa migrate onshore from deeper—or open—oceanic environments and undergo diversification to fill niches vacated by extinction of lineage A taxa. Taxa used to define the base of each successive biozone are indicated by heavy lines. Use of "A" and "B" in the diagram is not related to the use of letters to designate Lower Silurian brachiopod biozones.

higher pressure, darker waters of a deeper environment to shallow, unstable, warmer, lighter, and lower pressure waters of depauperate habitats involves not only movement of the stock but also adaption (evolution) of the organism to different environmental conditions. The slow evolution of this genetically conservative group could easily take millions of years. It should be noted that the duration of the changing environment at a specific locality is short, perhaps less than 10,000 years (Palmer, 1979).

Figure 1 illustrates our concept of a biomere boundary. The boundary is diachronous and becomes progressively younger from the slope to the craton through time as extinctions of taxa followed migrating environmental changes. This diagram indicates that four significant features are associated with the biomere. First, in traditional interpretations, biozones A1 through A4 would all be considered geologically older than biozones B1 through B3, although portions of A3 and A4 are lateral biofacies (and temporally equivalent) to portions of B1, B2, and B3. Second, at any section (x, y, or z) one or more lineage biozones (based upon first occurrence) might be missing, and this might be ascribed incorrectly to the existence of a paraconformity. Third, taxonomic diversity is lowest just above the boundary, but then increases as new taxa evolve and occupy previously vacant habitats. Fourth, the time involved for the entire boundary event may encompass several biochrons and thus the boundary represents considerably more time than the acceptable diachroneity of chronostratigraphic boundaries; note that in any single location the event occurs much more rapidly. Attempts to use traditional methods of correlation for an interval characterized by a biomere event would yield spurious results since sections from geographically distant areas would contain differing biozonal sequences. This evidence might be used to suggest the existence of an unconformity or a paraconformity in areas where biozones appear to be "missing." Also, a stratotype for time intervals characterized by this type of boundary could be selected in a specific geographic location, but it could not be easily correlated with other regions.

Evidence from the fossil record for the Ordovician-Silurian boundary provides an

example for the concepts presented above; studies for the last 100 years using traditional techniques and assumptions have not produced a satisfactory chronostratigraphic horizon. Three difficulties in illustrating the above concepts are: 1) paleontological studies are commonly confined to one system and do not treat changes in taxa across boundaries; 2) few studies treat shelf to slope paleoenvironments for refined time intervals; and 3) detailed stratigraphic data (such as for the Upper Cambrian strata in the southern Great Basin) often are inconclusive or unavailable.

Ordovician-Silurian Boundary

Lapworth (1879) defined the Ordovician-Silurian boundary using graptolite successions occurring in a sequence of marine strata exposed in the British Isles. The graptolite successions used by Lapworth (1879) and by Ellis and Wood (1914–1918) are known from few sections and are poorly correlated with benthic fossils (Berry, 1976). In the last hundred years considerable efforts to correlate this boundary have resulted in the recognition of what appears to represent a worldwide unconformity in paleoenvironments of the shelf and craton (Berry and Boucot, 1970, 1972a, 1972b, 1973a; Ziegler et al., 1974; Talent et al., 1975). This unconformity coincides with an erosion surface in some areas, but is recognized solely by the absence of biozones in other areas, thus implying the existence of a paraconformity. Poorly understood benthic taxa associated with the boundary are of low diversity and have been assigned to the Ordovician Period or Silurian Period by various authors (review by Cocks and Price, 1975).

The Ordovician-Silurian boundary is characterized by the following features in various regions: 1) poorly distributed graptolite successions; 2) physical unconformity; 3) missing biozones (paraconformity); and 4) low diversity benthic faunas that have not been precisely correlated and appear to be diachronous. Recognition of a standardized boundary, synchronous or nearly synchronous on a global scale, has not been accomplished. We propose an alternative model that explains the apparent paraconformities and unusual temporal and spatial distribution of the benthic taxa, and that indicates the Ordovician-Silurian transition may represent a biomere boundary.

Graptolite Successions.—The Ordovician-Silurian boundary was originally defined on the basis of graptolite successions in western Europe, and similar successions have been reported from other areas (Berry and Boucot, 1970). The latest Ordovician is recognized by the occurrence of *Diplograptus anceps* and *Climatograptus prominenselongatus* (Riva, 1974; Williams, 1976). Basal Silurian graptolite biozones are *Akidograptus acuminatus* and, locally, *Glyptograptus persculptus* or other biozonal indicators. Other taxa, including conodonts, ostracodes, brachiopods, corals, trilobites, and cephalopods, have been correlated with the successions. A significant difficulty in correlation is that graptolites are rarely associated with shelly faunas, especially in Upper Ordovician and Lower Silurian rocks (Williams, 1969; Ingham and Wright, 1970; Berry, 1976). A further factor is that benthic shelly faunas were affected more strongly by bottom environmental conditions than were the graptolites, and different shelly faunas may be associated with the same graptolites. We have concluded that graptolites provide more accurate correlation for slope sequences (pelagic argillite-chert belt of Erdtmann, 1976) spanning the Ordovician-Silurian boundary. Recognition and correlation of this boundary in shallow-water carbonate or clastic sequences is difficult because graptolites were rarely preserved in these sequences.

Unconformities.—In areas containing shelly faunas, the Ordovician-Silurian boundary most commonly is considered to be unconformable (Berry and Boucot, 1970, 1972a, 1972b, 1973a; Ziegler et al., 1974; Talent et al., 1975). In many cratonic sections of North America the base of the Silurian reportedly rests unconformably on Upper Ordovician rocks (Berry and Boucot, 1970). This regional unconformity has been related to an Early Silurian regression associated with glaciation (Berry and Boucot, 1973b; Sheehan, 1973). In some areas evidence for an unconformity is based upon the reported absence of earliest Silurian (early and middle Llandoverian) fossils (Rexroad

et al., 1965; Rexroad, 1967:15–16), thus suggesting the existence of a paraconformity. Shallowing and erosion of shelf areas has been reported by Lenz (1976) for the northern Cordillera. However, evidence reported by Johnson and Potter (1976), Miller (1976), Dunham (1977), and Miller and Walch (1977) indicates that deposition was continuous across the boundary interval in the southern Cordillera.

Considerable difficulty in recognition of the boundary has been noted for the Cellon section (shelf sequence) in the Carnic Alps and the Welsh borderland (Walliser, 1964, 1971; Schönlaub, 1971; Aldridge, 1972, 1975). Shallow-water sequences (based upon brachiopod communities) are characterized by the absence of early Llandoverian shelly faunas and by the existence of an unconformity separating Ordovician and Silurian rocks. However, as we have noted, shelly fauna biozones are poorly correlated with deeper water graptolite faunas and the existence and stratigraphic position of these unconformities is not well established (note especially Schönlaub, 1971:37, fig. 2 for Cellon section).

Diachronous Benthic Faunas.—An example of a diachronous benthic fauna is the "Hirnantian fauna." This fauna is typically a low diversity assemblage of brachiopods and trilobites with other minor shelly elements and is known from Europe, Asia, and North America (Wright, 1968; Nikitin, 1971, 1976; Schönlaub, 1971; Cocks and Price, 1975; Lesperance and Sheehan, 1976). This fauna was originally used by Bancroft (1933) to define a stage of post-Ashgillian age, but Ingham and Wright (1970) placed the Hirnantian Stage in the Ashgillian. Cocks and Price (1975) and Lesperance and Sheehan (1976) indicated that the Hirnantian fauna appeared to be diachronous and therefore could not be equivalent to the Hirnantian Stage.

Published information indicates that the fauna ranges in age from Ashgillian to medial Llandoverian (Nikitin, 1971, 1976; Schönlaub, 1971; Cocks and Price, 1975; Lesperance and Sheehan, 1976). Nikitin reported a Hirnantian fauna in the central USSR associated with the graptolite *Glyptograptus persculptus*, indicative of the *G. persculptus* Biozone (=Zone 16) of the earliest Llandoverian. Cocks and Price (1975) did not consider Nikitin's fauna to be Hirnantian, but the faunal list includes *Mucronaspis* (*Dalmanitina*) *macronata*, *Eostropheodonta* aff. *squamosa*, *Dalamanella testudinaria*, and *Hirnantia* species, which, at the generic level, represent common Hirnantian taxa.

Further evidence of the age relationships of the fauna is in the Carnic Alps of Austria and Italy. Schönlaub (1971: fig. 2) illustrated a Hirnantian fauna interbedded and coexisting with the conodont *Amorphognathus ordovicica*, diagnostic of Late Ordovician (Ashgillian) age. Cocks and Price (1975) discussed the Hirnantian fauna from the St. Martin's Cemetary Horizon in Wales, which occurs above strata of Rawtheyan age (Late Ordovician) and below faunas of early Llandoverian age. Lesperance and Sheehan (1976) discussed the occurrence of a Hirnantian fauna in Quebec that lies above lower or middle Ashgillian and below Llandoverian beds and is associated with the graptolite *Cliograptus rectangularismedius* of Early Silurian age. They also presented evidence (1976:721) from the type locality suggesting that the Hirnantian fauna may be of early and medial Llandoverian age. From the foregoing we conclude that the Hirnantian fauna is a diachronous "community," as suggested by Cocks and Price (1975), and should not be used to define a time-stratigraphic unit.

A second example of a diachronous benthic or nekto-benthic fauna is the distribution of conodont biozones. Detailed conodont biozones for latest Ordovician and earliest Silurian time in North America are not well established. Sweet et al. (1971) recognized Late Ordovician faunas (Faunas 10, 11, 12) and Nicoll and Rexroad (1968) and Pollock et al. (1970) recognized Early Silurian biozones (*Panderodus simplex, Icriodina irregularis, Neospathognathodus celloni* Assemblage Biozones). These have been recognized in mid-continental cratonic paleoenvironments but are poorly known from offshore (shelf or slope) paleoenvironments.

The *Panderodus simplex* Assemblage Biozone was named by Pollock et al. (1970:746) for conodonts occurring in a sequence of rocks below the lowest occurrence of *Icriodella discreta* or *Icriodella* new species or the genus *Icriocina* and above

diagnostic Ordovician species. This biozone contains a low diversity assemblage of simple-cone species and, although considered earliest Silurian, also contains Ordovician species (Craig, 1969; Walliser, 1971; Barnes et al., 1973; Liebe and Rexroad, 1977:844). The *P. simplex* Biozone has not been recognized in rocks deposited in shelf or slope paleoenvironments, although Miller (1975, 1976) and Audell and Miller (1979) reported nondiagnostic simple-cone taxa above Upper Ordovician rocks and below upper Llandoverian rocks in the southern Great Basin (shelf).

From these examples we conclude that the Hirnantian fauna and the *P. simplex* Biozone are diachronous and geographically transgressive (and partially regressive) pioneer assemblages (definition of assemblage following Kauffman and Scott, 1976) that existed after other Ordovician taxa were eliminated. This pioneer assemblage is much like stage 4 (not time stratigraphic) of a biomere (Stitt, 1971*a*) or stage 1 of Palmer (1979), where the extinction of specialized forms occurred, but the generalists were not affected.

Brachiopod Distribution.—Sheehan (1973, 1975) discussed the abrupt changes in brachiopods that occurred across the Ordovician-Silurian boundary. He described Late Ordovician brachiopod faunas as containing many stenotopic species, especially those existing in shallow-water (cratonic) paleoenvironments. These species became extinct because of an "ecologic crisis" at the end of Ordovician time, although the precise dating is difficult to determine. New taxa in the Early Silurian were derived from taxa existing in the open ocean (off the continental platform) that migrated into the empty niches from offshore paleoenvironments. He also noted that the diversity of Early Silurian brachiopods was low and did not stabilize until late Llandoverian time. These abrupt faunal changes were attributed to the onset of glaciation and consequent regression that eliminated many Late Ordovician niches. However, the distribution and evolution of brachiopod taxa also provide significant support for our biomere model.

Discussion and Conclusions

The boundaries of time-stratigraphic (chronostratigraphic) units are based upon evidence from the fossil record. Implicit in their definition and recognition is the assumption that, despite homotaxis as described by Huxley in the 1800s, the boundaries are synchronous on a global scale. Since the first definition of the Ordovician-Silurian boundary by Lapworth (1879) to resolve previous conflict over the Cambrian-Silurian boundary, attempts to recognize and correlate this boundary on a worldwide scale have been difficult. This difficulty is reflected by the contradictory information that includes peculiar or unusual associations of taxa, and the ever-present "paraconformity" reported in the literature. We suggest that the paleontological evidence can be interpreted differently. The changes in biota were due to environmental changes that produced an episode of extinction with significant diachroneity but which are not necessarily related to changes in lithology. Therefore, the Ordovician-Silurian boundary may be interpreted as a biomere boundary.

In Figure 2 we show the traditional concept of the Ordovician-Silurian boundary (Fig. 2a) and two models (Figs. 2b, 2c) that illustrate the Ordovician-Silurian transition as a biomere boundary. Our interpretation of the traditional model (Fig. 2a) is based upon reported distribution of unconformities and biota. Using either of the two biomere boundary models (Figs. 2b and 2c), it is evident that in offshore areas (slope and shelf) currently recognized shelly faunas of Late Ordovician (Ashgillian) age would be absent

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Figure 2. Three interpretations of the Ordovician-Silurian boundary. a) Traditional interpretation illustrating continuous deposition in deeper water (slope) and unconformity in shallow water (shelf and craton). b) Biomere boundary, illustrating diachroneity and relationships of established biozones to the boundary. c) Biomere boundary, illustrating greater diachroneity. The Hirnantian fauna (dotted line) and *Panderodus simplex* Biozone (dashed line) are low diversity time-transgressive associations and are found with Ordovician and Silurian taxa. Actual position of the biomere boundary is approximate.
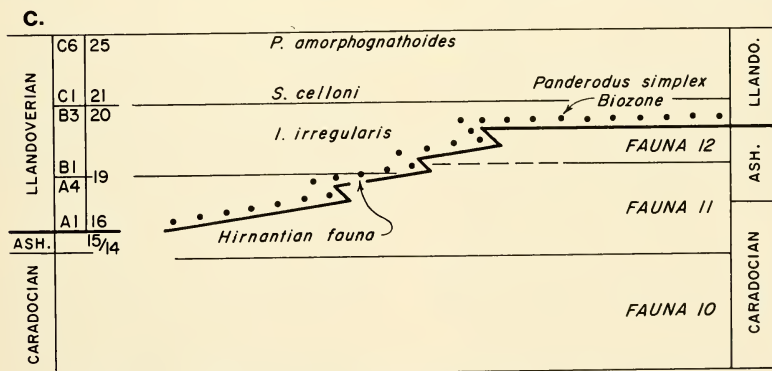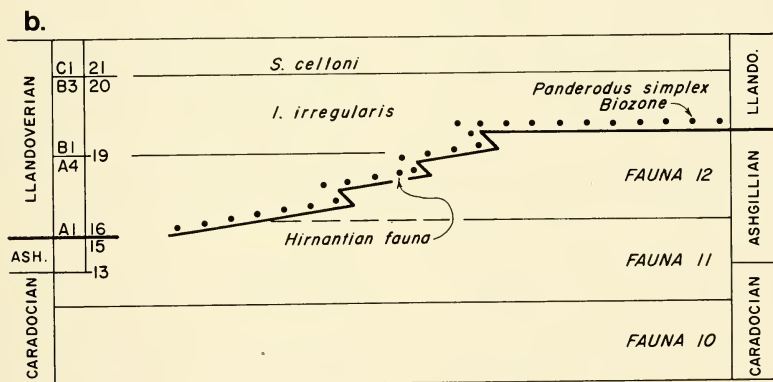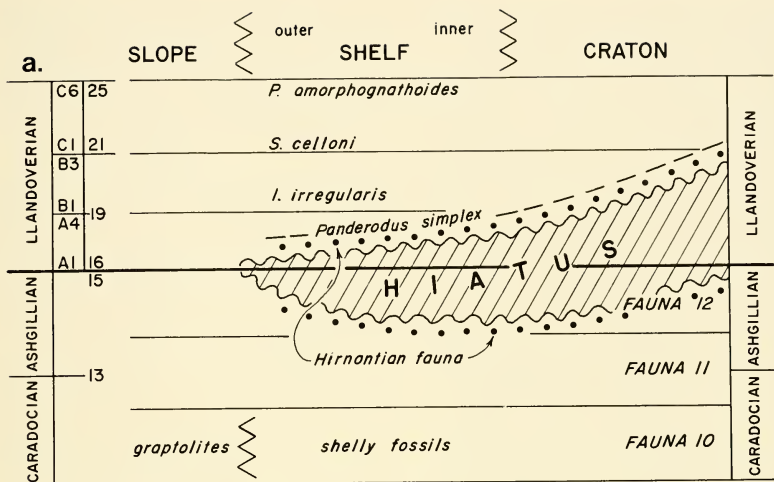
or only partially represented, but shelly faunas of Early Silurian (early and middle Llandoverian) age would be found. Onshore areas (craton) would contain faunas of Ashgillian age, but would lack currently recognized shelly faunas of early Llandoverian age. Not all of the data presented agree with the proposed models, but differences are generally minor and may be due to oversimplification in the diagrams. The influence of paleobiogeography was not taken into account; thus it may be necessary to construct other diagrams for different biotic provinces.

The existence of a biomere boundary would necessitate a redefinition of the systemic boundary. The most reasonable redefinition would establish the boundary at the base of the Ashgillian or at the base of the late Llandoverian and thereby employ well-established sequences of shelly faunas as well as graptolites. Another possibility would be to retain the traditional definition of the Ordovician-Silurian boundary based on typically "Ordovician faunas" and "Silurian faunas," and recognize that the boundary is diachronous, and therefore not a chronostratigraphic boundary. The recognition of the boundary would be based on different defining and/or characterizing taxa in different depositional settings (slope, outer and inner shelf, and craton).

Biomeres and biomere boundaries have been documented in the Cambrian and for the Cambrian-Ordovician boundary (Stitt, 1971b; J. F. Miller, *unpublished data*). In our study a biomere boundary is suggested for the Ordovician-Silurian boundary. Other boundaries in the Phanerozoic time scale may prove to be biomeres. Other possible biomere boundaries revealed by a brief survey of the literature include the Permian-Triassic, Triassic-Jurassic, Jurassic-Cretaceous, and Cretaceous-Paleogene.

Recognition of a major biomere boundary would require detailed measurements of strata and descriptions of taxa across the proposed boundary from a number of sections in deep-water (slope), shallow–water (shelf), and craton paleoenvironments. These sections should be taken as close as possible along a single paleolatitude; auxiliary sections should be located normal to the first line of sections and ideally should cover a significant band of latitude. Although suffering from a lack of many detailed studies, the widespread Paleozoic rocks in the western United States (Cordilleran region) represent slope, shelf, and craton paleoenvironments (Stewart et al., 1977); and these could provide the data necessary to document the existence of biomere boundaries.

Although biomeres currently have important stratigraphic implications only for Cambrian rocks, we suggest that the fossil record for younger strata supports expansion of the concept to include larger events on a global scale. These biomere boundaries represent major stratigraphic markers and have not been recognized through most of the Phanerozoic rock record, and they provide a new explanation for the lack of correlations of many traditionally defined chronostratigraphic and geochronologic boundaries.

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